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Fitness consequences of personality in the North American red squirrel (*Tamiasciurus hudsonicus*)

by

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ABSTRACT

Recent ecological research has demonstrated that animal personality is widespread, heritable, and has potentially important fitness consequences. Much conceptual work has focused on how variation in personality is maintained within populations, but empirical studies are lacking. I used female North American red squirrels (*Tamiasciurus hudsonicus*) in Kluane, Yukon, to investigate the fitness consequences of personality over multiple years and determine whether balancing selection or correlations to life-history tradeoffs may maintain its variation. Activity and aggressiveness were consistent within and variable among individuals. Maternal activity was correlated with offspring growth, while aggressiveness was correlated with offspring survival, but the direction and magnitude of relationships varied between years. Activity was also correlated with risk-taking, resulting in an apparent tradeoff: increasing activity reduced survival but increased the probability of fitness-enhancing bequeathal. Personality has significant fitness consequences in this population, and both balancing selection and correlations with life-history tradeoffs may maintain its variation.

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CHAPTER I

GENERAL INTRODUCTION AND THESIS OVERVIEW

PERSONALITY IN WILD POPULATIONS

The potential importance of animal personality to studies of behaviour and ecology has been recognized for decades but until recently only rarely tested in an ecological context (Wilson *et al.* 1994; Sih *et al.* 2004a). Individual variation in behaviour around a population or species mean has generally been viewed as non-adaptive "noise" rather than as a potentially adaptive product of natural selection (Wilson 1998). However in recent years, researchers have shown that these individual behavioural differences, known as personality, temperament, or behavioural syndromes, are consistent and associated with moderate heritability and significant fitness consequences in a wide variety of taxa (Réale *et al.* 2000; Dingemanse *et al.* 2002; Réale & Festa-Bianchet 2003; Dingemanse *et al.* 2004; Sih *et al.* 2004a; van Oers *et al.* 2004a; van Oers *et al.* 2004b; Carere *et al.* 2005; Sinn *et al.* 2006). Personality has also been shown to be associated with physiological and neuroendocrine differences among individuals, especially those related to the stress response such as adrenaline, noradrenaline and corticosterone (Koolhaas *et al.* 1999), and it appears that this common hormonal control may underlie correlations among personality traits as well as correlations of personality to life history, morphology and other traits (Koolhaas *et al.* 1999; Sih *et al.* 2004b). The recognition of the genetic and physiological bases of

personality has resulted in a surge of interest among ecologists, particularly because of the potential evolutionary consequences of these findings.

Personality has frequently been observed to be correlated through time and across contexts (Silverin 1980; Wilson *et al.* 1993; Koolhaas *et al.* 1999; Réale *et al.* 2000; Dingemanse *et al.* 2002; Sih *et al.* 2003; Sih *et al.* 2004b; Carere *et al.* 2005; Groothuis & Carere 2005; Johnson & Sih 2005; Duckworth 2006; Sinn *et al.* 2006; Bell & Sih 2007; Martin & Réale 2007). This means that there is significant individual consistency, and that individuals tend to behave in a certain way; for example, the most active individual in a feeding context may also be the most active in an exploratory context (Gosling 2001; Sih *et al.* 2004b). Different personality traits are frequently correlated as well, and these behavioural syndromes, or suites of correlations, have been observed in many different species (Sih *et al.* 2004b). In the proactive-reactive syndrome, for example, the most active individuals also tend to be, in a variety of contexts, aggressive, exploratory, bold, and active manipulators of their environment (proactive), while less active individuals are also less aggressive, slower to explore novel stimuli, and reactive to their environment rather than manipulative of it (reactive, Koolhaas *et al.* 1999; Sih *et al.* 2004a). These correlations could have the effect of limiting behavioural plasticity, leading to sub-optimal behaviours in some circumstances (Sih *et al.* 2004b; Johnson & Sih 2005). Studying the proximal, functional, developmental and historical explanations for these behaviours should allow us to understand when and why these syndromes occur, even when they sometimes appear to be maladaptive (Bell 2007b). Recent evidence suggests that predation plays a role in causing and maintaining correlations between boldness and aggressiveness (Bell & Sih 2007).

THE MAINTENANCE OF INTERINDIVIDUAL VARIATION

Given that personality is heritable and acted on by selection, the persistence of a range of personalities, rather than selection for a single best strategy in a species or population, is poorly understood (Dall *et al.* 2004; Groothuis & Carere 2005; Bell 2007a; Penke *et al.* 2007; Wolf *et al.* 2007). Psychological and physiological studies of laboratory animals often consider these personality differences to be alternative strategies aimed at environmental control that are usually equally successful (Koolhaas *et al.* 1999). However, some field studies have shown variation in the fitness of different behavioural types in time or space (Fraser *et al.* 2001; Réale & Festa-Bianchet 2003; Dingemanse *et al.* 2004; Höjesjö *et al.* 2004), reaffirming the question of how variation in personality is maintained when it is acted on by selection. Much of the recent conceptual research on personality has focused on this question, but few empirical studies have investigated it.

Two non-exclusive models have emerged that may explain the maintenance of variation in personality in natural populations. The first suggests that balancing selection, the change in selection regimes in time or space that results in all individuals having equivalent fitness overall, may maintain variation in personality (Penke *et al.* 2007). Balancing selection can take a number of forms, including overdominance (heterozygote advantage), antagonistic pleiotropy, fluctuating selection due to environmental heterogeneity, and negative frequency dependence (Penke *et al.* 2007). Antagonistic pleiotropy, a trait that has a positive effect on one aspect of fitness and a negative effect on another, could act to maintain variation when a single trait has different effects on different aspects of fitness (Schluter *et al.* 1991), or when two or more behaviours that are

correlated as part of a behavioural syndrome are subject to opposing selection pressures (Bell & Sih 2007). In wild populations, environmental heterogeneity might act to maintain variation in personality (Mangel 1991; Penke *et al.* 2007). Differences in resource supply, habitat structure, predation regimes, or other environmental factors could, in conjunction with overlapping generations (Ellner & Hairston 1994), result in selection maintaining rather than reducing variation. For this to occur, the phenotypes at each extreme must be favoured under different conditions and have exactly equal fitness at some point (Penke *et al.* 2007). Additionally, the effects of balancing selection must be stronger than those of any other selective regime, such as directional selection (Turelli & Barton 2004; Penke *et al.* 2007). These requirements of balancing selection make it difficult to demonstrate. The accumulation of data over many years with varying environmental conditions would be needed to show that individuals at both ends of the phenotypic spectrum leave an equal number of descendents many generations down the line.

A second potential mechanism focuses on the relationship between life-history trade-offs and personality. Wolf *et al.* (2007) use the example of a tradeoff between reproduction and survival, where some individuals begin reproducing early while others delay reproduction in order to acquire a greater number of resources. They suggest that individuals that reproduce early have much to gain by being risk-prone in a variety of circumstances in order to maximize their immediate acquisition of resources, whereas individuals that delay reproduction should be generally risk-averse because they must ensure their survival until reproduction. Wolf *et al.* (2007) used an evolutionary model to show that this correlation between life-history and behaviour leads to individuals

behaving both consistently and differently from each other, and to behaviours related to risk-taking, such as activity, aggressiveness and boldness, being correlated. Therefore, when there are life-history trade-offs that individuals resolve differently, selection could act to maintain the personalities that are correlated with those tactics (Wolf *et al.* 2007). A similar trade-off between growth and mortality to affect risk-taking behaviours, and hence personality, has also been suggested (Stamps 2007), and probably the outcome could be the same for many different life-history traits that are subject to trade-offs. Another related idea proposes that personality differences are a result of state-dependent behaviour (Dall *et al.* 2004). An individual's state may be related to its health, territory quality, or life-history, for example, and as long as that state remains constant, so should the animal's personality, which could then be maintained by virtue of its correlation to state (Dall *et al.* 2004; Bell 2007a). However, when personality is heritable, it is not clear why the correlation would remain without the action of another mechanism.

Domestication experiments on silver foxes (*Vulpes vulpes*) have shown that many morphological, physiological, developmental and life-history traits change in association with selection on behavioural traits such as tameness (Trut 1999). A few studies on wild populations have also found correlations between life history parameters and personality traits (Réale *et al.* 2000; Armitage & van Vuren 2003). The concept of correlations between personality traits and life-history is therefore not unprecedented, and the correlations may even have a genetic component. Of course, if this is the case, then the question of why variation in life-history strategies are maintained simply replaces the question of why personalities are maintained.

Probably both of the mechanisms discussed above are involved to a certain extent in the maintenance of variation in personalities in the wild. However, few empirical studies have examined any aspect of these models, and in particular, studies of the fitness consequences of personality that span multiple years and multiple life history traits are needed in order to begin to understand the forms and variability of selection pressures and the patterns of relationships between personality and life history.

The primary objective of my thesis research was to investigate the fitness consequences of personality and potential mechanisms for the maintenance of variation within populations. Although previous research suggests that personality influences many aspects of life history, I have used a combination of behavioural field studies and long term life-history data in order to investigate two aspects in particular, the effects of maternal personality on the growth and survival of offspring, and the relationship between personality and risk-taking behaviours.

MATERNAL EFFECTS AND CONSEQUENCES FOR OFFSPRING FITNESS

An interesting aspect of personality in wild populations is the potential for indirect genetic effects on offspring fitness acting via maternal behaviour. Maternal behaviour has been shown to be related to her personality in a number of species, and it seems that different behavioural types frequently have different parental styles (Fairbanks 1996). Proactive parents (aggressive, bold or active) often appear to engage in parental care activities less frequently, or less effectively (Silverin 1980; Duckworth 2006; Gammie *et al.* 2006). This may be a result of behavioural carryover from contexts in

which high aggressiveness is beneficial, such as territory defence, to contexts in which it is not, such as caring for offspring (Sih *et al.* 2004b). This carryover could be a result of different hormonal profiles of proactive and reactive parents, leading them to allocate their time differently and spend more time in activities such as territorial defence and less time in offspring care (Silverin 1980; Duckworth 2006). In other cases, proactive parents are seen to spend more time in parental activities, but still have reduced performance (Benus & Röndigs 1996; Westergaard *et al.* 2003; Cleveland *et al.* 2004). There are also cases, however, where proactive parents show higher reproductive success or higher levels of parental care (Budaev *et al.* 1999; Réale *et al.* 2000). In biparental species, the interaction between parental personalities can be important, and assortatively mated pairs tend to be most successful, producing more recruits (Dingemanse *et al.* 2004) or fledglings in better condition (Both *et al.* 2005), or having improved hatching success (Sinn *et al.* 2006). Both *et al.* (2005) suggested that reactive individuals (slow explorers) may be better parents because they respond to changes in the environment more effectively, while proactive parents may acquire better territories and provide better resources.

There may also be differences in the energy requirements of proactive and reactive individuals and their offspring, which could affect both parental behaviour and offspring response. Increased metabolic rates have been reported in fish in association with high plasma concentrations of the metabolically-active form of testosterone, 11-ketotestosterone (Ros *et al.* 2004), and also with the rate of aggressive behaviours (Ros *et al.* 2006). Additionally, higher levels of prenatal testosterone lead to higher resting metabolic rates in nestling zebra finches (Tobler *et al.* 2007). If personality is heritable,

then both proactive parents and their young may have higher-than-average energy requirements, and proactive parents could potentially have trouble meeting the nutritional needs of their young even if they provide increased care. This may be apparent in offspring growth rates, but that has not been examined to date. Alternatively, the outcome could be resource-dependent, such that proactive individuals have particularly high success when food is abundant, but particularly low success when it is scarce.

Only a few studies have examined whether the effects of personality on reproductive success change with resource availability between years (e.g. Dingemanse *et al.* 2004; Both *et al.* 2005), and those studies have focused on a small number of personality and life history traits. Studies encompassing multiple life history traits and multiple years are needed in order to clarify the effects of food abundance and personality on offspring fitness, and also to determine whether there are trade-offs among these traits.

HABITAT USE AND MORTALITY RISK

Personality is frequently associated with differences in risk-taking behaviours and survival. Proactive individuals tend to be more willing to take risks, leading them to be more likely to disperse (Fraser *et al.* 2001; Dingemanse *et al.* 2003; Cote & Clobert 2007), to forage under predation risk (Coleman & Wilson 1998; Sih *et al.* 2003; Biro *et al.* 2004; Bell & Sih 2007; Reaney & Backwell 2007), and to live in human-disturbed habitat (Martin & Réale 2007). They also tend to have larger territories (Watson & Miller 1971; Civantos 2000) and faster growth rates (Biro *et al.* 2004). However, these increases in risk-taking behaviours often entail a high risk of mortality due to predation

(Fraser *et al.* 2001; Biro *et al.* 2004; Bremner-Harrison *et al.* 2004; Biro *et al.* 2006; Bell & Sih 2007). There are also cases, however, in which more proactive individuals have been reported to have lower mortality (Godin & Davis 1995; Civantos 2000; Réale & Festa-Bianchet 2003), or in which the relationship varies with environmental variables [e.g. resource abundance (Dingemanse *et al.* 2004), habitat complexity (Höjesjö *et al.* 2004), predation regime (Biro *et al.* 2004; Brown *et al.* 2005; Biro *et al.* 2006)]. There seems to be a number of factors involved in these patterns. Proactive individuals engage more often in risky behaviours, and so are at increased risk of predation but only if predation pressure is fairly high. However, they are also more likely to engage in predator inspection, which reduces the likelihood of attack (Godin & Davis 1995). They may have higher energy requirements and therefore be more likely to starve when resource levels are low (Ros *et al.* 2004; Ros *et al.* 2006; Tobler *et al.* 2007), but they may also be able to defend better territories or resources (Civantos 2000; Both *et al.* 2005).

Although patterns are starting to emerge regarding the relationship between personality, risk-taking and mortality, little of this research has examined habitat usage in territorial species. While extra-territorial movements tend to entail higher risk of mortality (Metzgar 1967; Larsen & Boutin 1994; Stuart-Smith & Boutin 1995), they may also confer benefits ranging from knowledge of vacant territories to copulations to foraging opportunities (Neudorf *et al.* 1997; Bruinzeel & van de Pol 2004; Fedy & Stutchbury 2004; Gerhardt 2005; Pedersen *et al.* 2006). If proactive individuals are more willing to take risks, and therefore leave their territories more readily or more frequently,

then there may be measurable costs and benefits associated with these behaviours, including increased risk of mortality.

STUDY SYSTEM

North American red squirrels (*Tamiasciurus hudsonicus*) provide an excellent system for investigating the fitness consequences of personality. They are diurnal, tree-dwelling sciurids that defend individual food-based territories year-round (Smith 1968; Gurnell 1984). Their reproductive fate and survival can be followed readily owing to their territorial nature, conspicuous behaviours, and trappability. The accessibility of their nests make it possible to enumerate, mark and track the fates of offspring starting immediately after birth. Northern populations of red squirrels experience yearly fluctuations in food availability resulting from variable white spruce (*Picea glauca*) cone crops (LaMontagne & Boutin 2007), making this a good system in which to examine whether selection pressures on personality are resource-dependent. Mast years cannot be reliably predicted, but generally occur every 5-7 years, meaning that a large number of females experience breeding in both high food years and low food years.

The ecology, life-history, and behaviour of red squirrels are well studied. Parental care is solely maternal, and offspring traits are strongly influenced by maternal as well as environmental effects (Humphries & Boutin 2000; McAdam *et al.* 2002; McAdam & Boutin 2003a; Réale *et al.* 2003a; Réale *et al.* 2003b; McAdam & Boutin 2004). Most young are born between March and June, and both average parturition date and average juvenile growth rate depend on the previous year's cone abundance (Humphries & Boutin

2000; McAdam & Boutin 2003a; Réale *et al.* 2003a; Réale *et al.* 2003b; Boutin *et al.* 2006). Selection on nestling growth rates has been shown to vary in magnitude and direction between years (McAdam & Boutin 2003b). Juveniles emerge from the nest around 40 days of age and wean at 70 days (Humphries & Boutin 1996; McAdam *et al.* 2007), after which they either settle on a portion of their mother's territory or disperse and establish their own (Price *et al.* 1986; Boutin & Schweiger 1988; Boutin *et al.* 1993; Price & Boutin 1993; Berteaux & Boutin 2000; Boutin *et al.* 2000). Offspring that are bequeathed a territory by their mother are more likely to survive the winter and enter the breeding population the following year (Boutin *et al.* 1993; Berteaux & Boutin 2000), and so bequeathal has a positive effect on the mother's fitness.

Predation is a major cause of mortality in both adults and juveniles (Stuart-Smith & Boutin 1995). The main predators in the study area are lynx (*Lynx canadensis*), coyote (*Canis latrans*), great horned owl (*Bubo virginianus*), and northern goshawk (*Accipiter gentilis*) (Stuart-Smith & Boutin 1995). Predators often leave conspicuous kill sites that include fur, tails, eartags, and radio collars, and so the fate of a dead squirrel is often known with certainty. Juveniles are more likely to be predated while off the natal territory (Larsen & Boutin 1994), but it is not known if this is the case for adults. Behaviour plays an important role as well, and individuals that spend less time vigilant or resting and more time in exposed locations are more likely to be predated (Stuart-Smith & Boutin 1995; Anderson & Boutin 2002).

THESIS CHAPTERS

This thesis is comprised of two data chapters. Chapter II is entitled "The interaction between personality, offspring fitness and food abundance in North American red squirrels" and has been accepted for publication in Ecology Letters (Boon *et al.* 2007). It describes in detail the field and statistical methods used to measure personality, and defines the behaviours used in assessing personality. It also describes the behavioural syndrome that is observed in this system, and relates the personality of mothers to the growth and survival of their offspring in multiple years. The results suggest that balancing selection may play a role in maintaining variation in personality.

Chapter III, "Personality, habitat use and their consequences for survival in North American red squirrels", relates personality to risk-taking behaviours and extra-territorial movements in the wild. It suggests that there is a trade-off associated with risk-taking behaviours, such that they lead to reduced survival and increased probability of predation, but also an increased probability of territory bequeathal to offspring, which increases the juvenile's chances of overwinter survival.

Together, these chapters provide an overview of personality in red squirrels and its implications for the behaviour and life history of individuals. They also provide evidence that selection is actively maintaining variation in personality within a wild population through balancing selection. The last chapter, Chapter IV, is a general conclusion and suggests next steps in the study of personality.

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CHAPTER II

THE INTERACTION BETWEEN PERSONALITY, OFFSPRING FITNESS, AND FOOD ABUNDANCE IN NORTH AMERICAN RED SQUIRRELS

INTRODUCTION

Animal personality refers to consistent individual differences in behaviour (Sih *et al.* 2004), and it has been demonstrated to be repeatable (Réale *et al.* 2000; Dingemanse *et al.* 2002; Carere *et al.* 2005), heritable (Dingemanse *et al.* 2002; Drent *et al.* 2003), and a predictor of several other ecological and social variables [e.g. dispersal distance (Dingemanse *et al.* 2003), parental care (Cleveland *et al.* 2004; Both *et al.* 2005; Duckworth 2006), territory size (Civantos 2000)]. However, we know very little about the fitness consequences of personality and about how the observed range of among-individual variation is maintained (Sih *et al.* 2004; Dingemanse & Réale 2005; Smith & Blumstein In review).

Only a handful of studies have examined the effects of personality on fitness. Bold bighorn ewes (*Ovis canadensis*) are less likely to be killed by cougars (*Puma concolor*, Réale & Festa-Bianchet 2003). The survival and reproductive success of great tits (*Parus major*) depends on an interaction between their exploration speed, sex, and winter resource availability, such that the direction of selection fluctuates between years (Dingemanse *et al.* 2004). The phenotype of the pair is also important, and assortatively

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mated pairs produce offspring in the best condition (Both *et al.* 2005). Reduced weaning or fledging success is associated with shyness in bighorn ewes (Réale *et al.* 2000), aggressiveness in male western bluebirds (*Sialia mexicana*, Duckworth 2006), and low concentrations of 5-hydroxyindoleacetic acid (5-HIAA, a serotonin metabolite) in rhesus macaques (*Macaca mulatta*), which is associated with low sociability, high aggressiveness, and more risk-taking behaviours (Mehlman *et al.* 1994, 1995; Westergaard *et al.* 2003).

Personality is also associated with differences in maternal behaviour that can affect fitness. Female house mice (*Mus domesticus*) selected for high aggression nurse and groom their pups more than females selected for low aggression (Benus & Röndigs 1996), but take longer to retrieve their pups in a behavioural trial (Gammie *et al.* 2006). Low 5-HIAA rhesus macaque mothers are highly protective and restrictive with their infants (Cleveland *et al.* 2004). Both *et al.* (2005) suggested that slow exploring great tits may be better parents, because they respond more easily to environmental change. Maternal behaviour has also been shown to produce persistent effects on the stress responses of offspring through epigenetic programming (Weaver *et al.* 2004). If the covariance of maternal style and personality is widespread, then it could result in important maternal effects on offspring growth and survival, leading to further fitness consequences of personality.

If personality indeed has important consequences for fitness, it would seem that selection should reduce variation in favour of all individuals having the same "optimal" personality. However, selection could actively maintain genetic variation in personality traits through balancing selection, in which different phenotypes are favoured under

different conditions, leading to identical average fitness overall (Penke *et al.* 2007). This could potentially result from fluctuations in the favoured phenotypes due to environmental heterogeneity in space or time (Mangel 1991; Dingemanse *et al.* 2004), and/or due to correlations between risk-associated personality traits and life history tradeoffs (Stamps 2007; Wolf *et al.* 2007). Variation in personality traits could also be maintained by having different effects at different stages during ontogeny, or on different components of fitness (Schluter *et al.* 1991), or there could be antagonistic effects of different personality traits that are correlated as part of a behavioural syndrome. Behavioural syndromes are the correlation of personality traits in different conditions or contexts, or the correlation of different personality traits to each other, such as aggressiveness and boldness (Sih *et al.* 2004). These phenotypic correlations may result from common hormonal control of behaviours or other forms of genetic correlation, which may constrain the optimization of any one personality trait, thereby maintaining variation in both traits (Sih *et al.* 2004).

In this study, we used *Tamiasciurus hudsonicus* Banks (North American red squirrel) to test whether personality affects fitness in a wild population over multiple years, and if so, whether the direction of selection pressures is consistent or variable. Red squirrels are diurnal tree squirrels with female-only parental care that defend non-overlapping food-based territories year-round (McAdam *et al.* 2007). They experience dramatic yearly fluctuations in their food supply resulting from mast-seeding of the dominant conifer in the region, the white spruce (*Picea glauca*, LaMontagne & Boutin 2007), and in our study area the average number of cones per tree has ranged from 0 to 982 in the last 20 years (S. Boutin unpublished data). Squirrels store cones in a central

food cache, or midden, and they rely primarily on this cached food through the winter and into the spring (Boutin *et al.* 2006). In one of the first studies to examine multiple life history traits in relation to personality in the wild, we measured personality in 98 females, and tested for effects on parturition date, litter size, offspring growth and survival in the nest, and offspring survival through their first winter, during both low- and high-cone years. We found that the optimal personality changes between years and according to the life history trait in question, and suggest that balancing selection may play a role in maintaining variation in personality in this population.

METHODS

Study site and population

This study was conducted in conjunction with a long-term study of North American red squirrels near Kluane National Park in southwestern Yukon, Canada (61° N, 138° W). We combined field studies of personality from summer 2005 with reproductive and life history data of those individuals from 2003 to 2006. Individual squirrels were followed in detail as described in Boutin *et al.* (2006) and McAdam *et al.* (2007). Briefly, all individuals on three study grids (two control and one food supplemented) were marked with numbered ear tags threaded with a unique combination of coloured wires for identification at a distance. On the food supplemented grid, each squirrel in the population was provided with *ad libitum* peanut butter from fall until spring, in a bucket hung above the primary midden. Survival and reproductive status of squirrels were monitored through behavioural observations and regular live trapping with

Tomahawk traps. Soon after parturition, we located females' nests with telemetry and briefly removed the young to sex, mark and weigh them. We reentered the nests when the juveniles were between 25 and 30 days old to weigh and mark them with ear tags. Juveniles emerge from the nest at approximately 40 days and wean at 70 days (McAdam *et al.* 2007). Survival of juveniles after emergence was monitored using live trapping, behavioural observations, and telemetry.

Personality tests

We measured personality in 71 adult females and 27 juvenile (young of the year) females with three behavioural tests. The first was an open field (OF), which is used to quantify activity, exploration, and stress responses in a novel environment (Walsh & Cummins 1976; Martin & Réale 2007). The second test, a mirror-image stimulation (MIS), is used to assess aggressive and sociable behaviours (Svendsen & Armitage 1973). The two tests were performed in the same testing session, with the OF also serving as habituation time before the MIS (Svendsen & Armitage 1973). The testing arena was a 60cm x 80cm x 50cm white box with a clear acrylic lid through which the behavioural trials were recorded with a digital video camera. A series of four blind holes in the floor aided in separating exploratory behaviours from activity, since they are generally correlated (Martin & Réale 2007). A 45cm x 30cm mirror fixed to one end of the arena was covered during the OF and exposed for the MIS. All tests were performed at the point of capture on the territory of the focal individual, and were conducted by the same observer (AKB) using a standardized procedure.

The focal squirrel was captured, handled, and transferred to a trap leading into the arena. The 7.5-minute OF trial began when the squirrel entered the arena. The five-minute MIS trial started after uncovering the mirror, when the squirrel was perceived to have seen its reflection. Its behaviour changed markedly when it saw its reflection, and generally it either froze suddenly while looking at the mirror, or approached and attacked the mirror in rapid succession (personal observation, AKB). At the conclusion of the trial, the squirrel was released and the arena cleaned with 70% ethanol. Of the 71 adult females, 55 were retested six or more weeks later; of the 16 that were not retested, seven died of natural causes, two disappeared, and seven were alive but could not be recaptured. The 27 juveniles were tested as soon as they could be trapped (mostly 70-85 days of age; range 51 to 108 days). Subsequent analyses showed that age of juveniles at the time of testing had no effect on personality (analysis not shown). Juveniles were tested only once due to the short time interval between first trials and the end of the field season.

The videotaped trials were analyzed using The Observer Video-Pro 5.0 (Noldus Information Technology, Wageningen, The Netherlands). For the OF, we used an ethogram similar to that of Martin and Réale (2007) for the Eastern chipmunk (*Tamias striatus*), and for the MIS we developed one based on our observations and previous descriptions of agonistic behaviours in the red squirrel (Ferron 1979, 1980). See Table 1 for more details of the behaviours measured.

The third behavioural test quantified the squirrel's response to handling (Carere & van Oers 2004). Immediately after transferring an individual from a trap to a handling bag, we measured struggle rate (number of seconds spent struggling in 30 seconds) and

breathing rate (breaths per 10 seconds). Between one and seven samples were collected per individual, by five observers.

Statistical analyses

For the OF and MIS, we used principal components analyses (PCA; separately for the two tests) to reduce the number of behaviour variables measured to a limited number of synthetic behavioural variables, following Martin and Réale (2007). This allowed us to identify the primary differences among individuals along those behavioural axes using linear mixed models (LMM) with the synthetic variables (principal component scores) as dependant variables, plus age, reproductive condition, grid of origin, testing date and time, and trial number as fixed effects, and squirrel identity (ID) as a random effect. For each synthetic variable, we used stepwise backwards elimination model selection on the mixed model, compared it to a linear model without ID using a likelihood ratio test with one degree of freedom, and determined the repeatability, or proportion of variance due to the individual (Lessells & Boag 1987). For components with a repeatability significantly greater than zero (i.e. a significant effect of individual in the mixed model), we extracted the best linear unbiased predictors (BLUPs), which provide predictions of the random effect of each individual squirrel independent of the other terms in the model, standardized to a mean of zero (Kruuk 2004). We used these BLUPs as individual values of "personality traits" in further analyses. To simplify the analysis and interpretation of life history models, we chose to include only the first principal component from the OF and the MIS. These two variables represent activity/exploration (OF1) and aggressiveness (MIS1), as described in the Results section, and were chosen because of

their potential importance to the ecology of squirrels in terms of energetics and the ability of a squirrel to obtain and defend food resources (M. M. Humphries, unpublished data, Stuart-Smith & Boutin 1994).

For struggle rate and breathing rate, we used LMMs in the same way to test and control for micro-environmental and individual characteristics, to estimate repeatability, and to reduce multiple observations to a single value per individual. In each model we included squirrel ID as a random effect, plus age, grid, reproductive condition, test date, and observer as fixed effects. We extracted the BLUPs and used these as the individual values of struggle and breathing rate in further analyses.

To determine whether squirrels exhibit behavioural syndromes, we tested for correlations among OF1, MIS1, struggle rate, and breathing rate using Pearson's product moment correlations in a pair-wise manner among the 4 variables. False discovery rates were calculated to account for multiple comparisons (Benjamini *et al.* 2001). Positive correlations among these four traits would indicate a "proactive-reactive" syndrome (Koolhaas *et al.* 1999; Sih *et al.* 2004).

We investigated the effects of personality on the following life history traits: 1) parturition date; 2) litter size at birth; 3) offspring growth rate; 4) survival of offspring in the nest; 5) overwinter survival of offspring; and 6) territory bequeathal. In initial models, we included other variables that have previously been found to be important in this system (see McAdam *et al.* 2002; McAdam & Boutin 2003a, b) such that significant effects of personality on life history traits would be independent of those variables. Because they were included only to avoid confounding results regarding personality, we will not discuss them in any detail. The fixed effects included in most initial models were

year, grid, female's age, activity, aggressiveness, and the interactions year by activity, year by aggressiveness, and activity by aggressiveness. These are referred to collectively as the standard fixed effects, and any additional fixed effects are indicated in the description of each model.

We used stepwise backwards elimination model selection with variables standardized to a mean of zero, and all analyses were performed using R (R Development Core Team 2006). Sample sizes vary according to the number of individuals or litters for which we had complete data in each analysis. Because individual females were observed over multiple years, we included female ID as a random effect in all of the following analyses. This allowed us to avoid pseudoreplication and to estimate the proportion of variance of a trait that is due to individual effects. Variance among females represents genetic (both additive and non-additive) and maternal effects that could not be explained by the fixed effects included in the model (Falconer & Mackay 1996). Therefore, the effect of a personality trait on offspring fitness could be interpreted independently of other potential genetic and maternal effects.

For some of our analyses, we used generalized linear mixed models with penalized quasi-likelihood (glmmPQL function). These models are not fit using log-likelihood methods, and so likelihood ratio tests cannot be used to evaluate the strength of fixed effects. Because our initial models are complex, we used a conservative strategy of first employing a GLM to reduce the number of interactions and fixed effects. We then used the terms included in this final GLM as the baseline from which to evaluate the data using a GLMM to account for mother's ID as a random effect, and further simplified the GLMM using t-tests, retaining the categorical variables when at least one level differed

significantly from the others, to obtain our selected model. We also verified our analyses using another method, GLMMs using the lmer function followed by Markov Chain Monte Carlo simulation to calculate confidence intervals. We determined that (1) all fixed effects in our final GLMMPQL models are also significant in an lmer model with MCMC simulation, and (2) our methods appear to be more conservative, but do not greatly alter the interpretations, and we feel that they allow a more intuitive understanding of the results.

To model parturition date (of a female's first litter in each year), we fit an LMM (years 2003-2006; n = 158 litters produced by 80 females) with the standard fixed effects.

We analysed litter size at birth (years 2003-2006; n = 175 litters produced by 80 females) first with a GLM with quasi-Poisson errors and a log link function, and included the standard fixed effects plus parturition date. As described above, we then included the variables that remained in that model in a GLMM with the same error structure, and further simplified the model.

The effects of a female's personality on the growth rate of her offspring in the nest (i.e. gain in mass between first and second measurement divided by the number of days; years 2003-2006, n = 348 offspring produced by 75 females) was examined using an LMM with the standard fixed effects plus parturition date, juvenile sex, juvenile mass at first measurement, and litter size at second measurement.

The survival of juveniles in the nest (i.e. from shortly after birth until shortly before emergence; years 2003-2006, n = 517 offspring produced by 79 females) was analysed using a GLM followed by a GLMM, with binomial errors and a logit link

function. The standard fixed effects plus parturition date, juvenile sex, and litter size and juvenile mass at first measurement were included in the initial model.

For the survival of offspring through their first winter (from weaning until May 1 of the following year; years 2003-2005, n = 124 offspring produced by 49 females), we also included information on territory bequeathal; mothers sometimes give their offspring part or all of the natal territory, which increases the probability of overwinter survival for the juvenile (Price & Boutin 1993; Berteaux & Boutin 2000). A juvenile was considered to have been bequeathed to if it settled on part of the natal territory. We used a GLM followed by a GLMM, with binomial errors and logit link, and the standard fixed effects plus parturition date, juvenile sex, and bequeathal.

Finally, we examined whether the tendency of a mother to bequeath territories to her offspring was related to her personality. We created a binomial variable indicating whether or not a female bequeathed part or all of her territory to at least one of her offspring, in each year for which she had at least one juvenile survive to weaning (n = 67 instances for 49 females). We did not include year in this analysis because of the small number of records for 2003 and 2004. We ran a binomial GLMM including parturition date, number of offspring surviving to weaning, activity, and aggressiveness.

RESULTS

Personality

Following the PCA, we retained three components from the OF and two from the MIS, which explained 58.0% and 58.6% of the total variance, respectively. The first

principal component from the open field (OF1) was characterized by behaviours of locomotion and exploration (Table 1), and will be referred to as activity hereafter. OF2 was characterized primarily by behaviours representing different aspects of exploration and may be a measure of impulsiveness, while OF3 was composed of behaviours related to the stress response of the animal (Archer 1973; Martin & Réale 2007). The first component of the MIS (MIS1) separated observations with high values of Attack Rate, Crouch Rate, and time in the Front of the arena, from those with high Approach Latency, Attack Latency, and time in the Back (Table 2-1). This component will be called aggressiveness hereafter. MIS2 separated Stretch and Attack Latency from time spent far from the mirror.

The three components of the OF and first of the MIS showed significant individual repeatability ranging from 37.4% to 68.2% (Table 2-1), but MIS2 was not significantly repeatable. Squirrels tended to be more active (OF1 more positive) with advancing date ($F_{1,53} = 5.8$, $P = 0.02$) but less active in the second trial than in the first ($F_{1,53} = 21.6$, $P < 0.0001$). OF2 was generally more negative in second trials (decrease in Jump / Hang, increase in Sniff / Hole / Chew; $F_{1,54} = 39.0$, $P < 0.0001$), and OF3 more negative with advancing date (decrease in Chew / Pellets, increase in Scan / Groom; $F_{1,54} = 28.2$, $P < 0.0001$). Squirrels also became less aggressive (MIS1 more negative) with advancing date ($F_{1,54} = 7.7$, $P = 0.008$). Both handling tests were significantly repeatable (struggle rate: repeatability = 35.7%, LRT = 33.98, $P < 0.0001$; breathing rate: repeatability = 42.4%, LRT = 38.80, $P < 0.0001$). There was a significant effect of observer for both tests (struggle rate: $F_{4,166} = 12.5$, $P < 0.0001$; breathing rate: $F_{3,171} =$

23.2, $P < 0.0001$), and breathing rate tended to increase with advancing date ($F_{1,171} = 51.6$, $P < 0.0001$).

There were significant correlations between activity and aggressiveness ($r = 0.54$, $df = 96$, $P < 0.0001$), activity and struggle rate ($r = 0.42$, $df = 94$, $P < 0.0001$), activity and breathing rate ($r = 0.23$, $df = 95$, $P = 0.02$), aggressiveness and struggle rate ($r = 0.30$, $df = 94$, $P = 0.003$), and struggle rate and breathing rate ($r = 0.53$, $df = 94$, $P < 0.0001$). There was no correlation between aggressiveness and breathing rate ($r = 0.07$, $df = 95$, $P = 0.49$). None of these correlations was affected by the calculation of false discovery rates (Benjamini *et al.* 2001).

Maternal effects and fitness

There was no effect of activity or aggressiveness on parturition date or on litter size at birth (all removed with $P \geq 0.2$); the final model for parturition date included only year ($F_{3,73} = 28.2$, $P < 0.0001$), age ($F_{1,73} = 8.5$, $P = 0.005$) and grid ($F_{1,73} = 5.3$, $P = 0.02$), while only year significantly affected litter size (all years compared to 2005: 2003 = 1.03 ± 0.07, $t_{92} = -1.73$, $P = 0.09$; 2004 = 0.99 ± 0.05, $t_{92} = -3.14$, $P = 0.002$; 2005 = 1.16 ± 0.03; 2006 = 1.17 ± 0.04, $t_{92} = 0.33$, $P = 0.74$).

The growth rates of juveniles were significantly affected by an interaction between female's activity and year, such that in some years the offspring of the most active females grew most quickly, while in other years they grew most slowly (Fig. 2-1; Table 2-2). There were also significant effects of parturition date, litter size at second measurement, and mass at first measurement. Female ID significantly improved the fit of the model (LRT = 178.1, $df = 1$, $P < 0.0001$) and explained 70.2% of the remaining

variance in growth rate, which includes heritability and maternal effects not included as fixed effects.

In three out of four years, the probability of offspring survival to tagging decreased with increasing female aggressiveness, but the magnitude of the effect varied with year (Fig. 2-2a; Table 2-3). Juveniles born later in the season were more likely to survive to tagging. Female ID improved the fit of the model (LRT = 60.7, df = 1, $P < 0.0001$) and explained 81.3% of the remaining variance in the final model.

In 2003 and 2005, the offspring of the most aggressive females were most likely to survive the winter, while in 2004 they were least likely to survive (Fig. 2-2b; Table 2-4). Juveniles who received a territory from their mother had a higher chance of survival (marginally), as did juveniles born earlier in the year. All variables that remained in the final GLM were also significant in the GLMM. Female ID explained 0% of the remaining variance in the GLMM and did not improve the fit of the model (LRT = 0, df = 1, P = 1), so we present the GLM as the final model (Table 2-4). A female's personality did not affect her tendency to bequeath, but the probability of bequeathal increased with the number of juveniles successfully weaned (0.98 ± 0.40, df = 17, t = 2.46, P = 0.02).

DISCUSSION

A female red squirrel's personality is correlated with the growth rates and survival of her offspring both in the nest and through their first winter, suggesting that personality may influence offspring phenotype and fitness. Variation in personality in this population could be maintained by opposing selection pressures at several levels.

Environmental heterogeneity, such as temporally fluctuating food abundance due to mast seeding of the white spruce (Boutin *et al.* 2006; LaMontagne & Boutin 2007), may favour different values of personality traits in different years, and accordingly, the magnitude and direction of the correlations among personality and fitness traits are not consistent, in some cases reversing between years. Selection pressures also depend on the particular life history stage and personality trait in question; while there is no effect of a female's personality on her parturition date or litter size, her offsprings' growth in the nest is affected by her activity, while their survival to tagging and overwinter are influenced by her aggressiveness. Selection pressures also appear to vary in direction or magnitude at different times during offspring development: the aggressiveness of a female can affect the survival of her offspring differently from birth to tagging than it does from weaning to spring (Fig. 2-2). Given the numerous opposing selection pressures, there is not one "best" personality that leads to the highest fitness in all conditions, and balancing selection may therefore favour the maintenance of variation in these traits (Schluter *et al.* 1991; Sih *et al.* 2004; Penke *et al.* 2007). Furthermore, recent theoretical models have suggested that under variable food conditions, the involvement of personality traits in life history tradeoffs may lead to the maintenance of individual differences in personality (Stamps 2007; Wolf *et al.* 2007).

Red squirrels show consistent individual behavioural differences, and the most active squirrels also tend to be the most aggressive, to struggle the most, and to have the highest breathing rate during handling. These phenotypic correlations among personality traits are typical of the proactive-reactive behavioural syndrome observed in other animals (Koolhaas *et al.* 1999; Sih *et al.* 2004), and have been found to be linked to

physiological and neuroendocrine differences in rodents, such as plasma concentrations of adrenaline, noradrenaline, and corticosterone (Koolhaas *et al.* 1999; Groothuis & Carere 2005). Although we do not have estimates of the genetic correlations, this may indicate that these traits are not evolutionarily independent.

The activity of a female affected the growth rate of her offspring, but the direction of the effect depended on the year. In 2003 and 2006, more active females had faster-growing offspring, in 2005 they were slower-growing, and in 2004 there was no effect. This may be a result of yearly differences in food availability. Both the current year's and the previous year's cone abundance have significant effects on juvenile growth rates (McAdam & Boutin 2003a). The average number of cones per tree on the two control grids combined was 84 in 2002, 17 in 2003, 24 in 2004, 502 in 2005, and 2 in 2006. The 2003 and 2006 breeding seasons, for which there were positive correlations between female activity and juvenile growth rate, followed the years with the highest cone numbers in the time period of this study, while 2005, in which there was a negative correlation, followed two successive years of very low cone numbers. Active females may therefore produce high juvenile growth rates in good conditions, but low growth rates in poor conditions. This could result from genetic differences in resource acquisition ability (including obtaining, processing, and transforming resources to usable energy) if high acquisition ability is costly (Reznick *et al.* 2000), such as by requiring resources to be abundant for success (Tessier *et al.* 2000). This could mean that active squirrels can acquire more resources and therefore have more energy to allocate to reproduction, as well as other aspects of life history, relative to less active squirrels, but only when resources are abundant. When resources are scarce, they may be unable to

deplete available resources to as low a level as less active squirrels [as in high vs. low acquisition *Daphnia* species (Tessier *et al.* 2000), and fast vs. slow exploring great tits (reviewed in Groothuis & Carere 2005)], leading to the observed pattern of variation in juvenile growth rates. Correspondingly, McAdam and Boutin (2003a) reported a large decrease in maternal effects on juvenile growth rates with food supplementation in this population, and suggested that even in very high natural food conditions, the ability of a female to acquire resources was a source of significant variation. In this study, we did not detect an effect of food supplementation in years of high natural food abundance. However, unpredictable mast seeding of white spruce may lead to balancing selection on activity in females due to differences in juvenile growth rates resulting from differences in the acquisition and allocation of resources among individuals. Strong inference regarding the link between food abundance and the personality-fitness relationship would only be possible by accumulating data over multiple years with varying food conditions.

The survival of juveniles in the nest depends on the aggressiveness of their mother but not her activity. There is no clear relationship with food resources, as increasing aggressiveness corresponded to a higher probability of juvenile mortality in the nest in the year following both the smallest and the largest cone crop (2005 and 2006). These survival differences may result from other environmental effects that we did not measure in this study, or they could be due to differences in maternal style. If aggressive females provide less care or less milk to the litter relative to its needs, there may be greater competition for resources within the nest leading to greater mortality. Although aggressive female house mice spend more time nursing and grooming their pups, their offspring do not grow faster (Benus & Röndigs 1996). The authors suggest that time

spent nursing may not be a reliable indication of milk transfer, or that the offspring of aggressive females may have higher metabolic rates due to higher testosterone levels, necessitating a greater quantity of milk (Benus & Röndigs 1996; Tobler *et al.* 2007). Female rhesus macaques with 5-HIAA concentrations indicative of high aggression and low sociability have higher rates of fetal and infant death despite being very protective of their offspring (Westergaard *et al.* 2003; Cleveland *et al.* 2004). Aggressive male western bluebirds feed their mates less frequently during incubation (Duckworth 2006), and male pied flycatchers (*Ficedula hypoleuca*) with experimentally increased testosterone show increased courtship and territorial activities and reduced feeding of nestlings (Silverin 1980), leading to lower fledging success in both cases. Aggressiveness is therefore associated with reduced juvenile survival in a number of species. However in the current study, that appears to be true only in certain years, and the mechanism of the association remains unclear.

The overwinter survival of juveniles was also affected by the aggressiveness of their mother. The offspring of more aggressive females were more likely to survive the winter following the 2003 and 2005 breeding seasons, but less likely to survive following the 2004 breeding season, independently of their birth date and of whether they were bequeathed a territory or secured one independently. Similarly to juvenile survival in the nest, there is no clear relationship with food availability, but the heritability of personality or maternal effects could be important. If personality has a significant heritable component, then the offspring of aggressive females may survive better in some years because they themselves are more aggressive, such as by allowing them to compete more effectively for territories or food resources. However, this may also depend on a variety

of other factors, such as population density. If aggressive juvenile squirrels have higher testosterone concentrations, then they may also have higher metabolic rates (Tobler *et al.* 2007), which could hinder their survival when food is scarce and favour it when food is abundant, especially if there are also differences in resource acquisition ability as discussed previously (Reznick *et al.* 2000). A female's aggressiveness could also lead to maternal effects that influence juvenile overwinter survival; it has previously been demonstrated in this population that maternal nutrition prior to juvenile emergence affects juvenile overwinter survival, independently of the juvenile's body size and territory quality (Kerr *et al.* 2007). Nutritional factors or differences in maternal behaviour that are related to aggressiveness could also lead to persistent maternal effects to influence juvenile overwinter survival in this study. The relative importance of the aggressiveness of the offspring and that of the mother cannot be disentangled at this time, but in any case, the favoured maternal phenotype changes from year to year.

Personality influences life history in numerous ways in this population. Selection pressures on personality seem to act in different directions in different years and at different life history stages. Environmental heterogeneity, correlations among personality traits, and trade-offs among their effects on life history may therefore be actively maintaining variation in personality via balancing selection, because there is no one value of personality that performs best in all conditions encountered.

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TABLE 2-1

PCA loadings for behaviours in two behavioural tests, an open field (axes OF1-3) and a mirror-image stimulation (axes MIS1-2) in female North American red squirrels. Units are the percentage of time spent in each behaviour, unless indicated otherwise, and bold type indicates behaviours that contributed importantly to a component. MIS behaviours are mirror-directed, and latencies are log-transformed. The significance of repeatability was tested by comparing mixed models including individual identity as a random effect to linear models without it, using a likelihood ratio test (LRT).

Behaviour	OF1	OF2	OF3	Behaviour	MIS1	MIS2
still	**-0.49**	-0.11	-0.07	attack rate **	**0.42**	-0.13
walk	**0.48**	0.10	-0.13	crouch rate ††	**0.42**	0.03
jump rate	**0.38**	**0.36**	-0.13	Front ‡‡	**0.42**	-0.01
sniff *	**0.34**	**-0.34**	-0.11	attack latency	**-0.40**	**0.41**
hole rate †	**0.29**	**-0.34**	-0.26	approach latency	**-0.39**	0.00
rear	**0.29**	-0.24	-0.05	back ‡‡	**-0.30**	**-0.35**
hang ‡	0.18	**0.55**	0.28	grunt §§	0.22	-0.10
chew §	0.08	**-0.30**	**0.56**	stretch ¶¶	0.15	**0.82**
scan	-0.03	0.26	**-0.49**			
groom	-0.04	-0.29	**-0.36**			
# pellets ¶	0.25	-0.14	**0.33**			
SD	1.83	1.28	1.18	SD	1.90	1.04
% total variance	30.4	14.9	12.7	% total variance	45.0	13.6
% Repeatability	41.0	68.2	41.5	% Repeatability	37.4	15.2
LRT (df=1)	10.32	27.77	11.83	LRT (df=1)	8.58	1.46
P	0.001	<0.0001	0.001	P	0.003	0.23

* sniff the floor or walls † put head in hole in the floor ‡ hang from top of walls § chew or scratch at floor or walls ¶ number of pellets left in the arena after the tests ** aggressive contact, standing on back legs and striking with the front (Ferron 1979) †† posture indicative of imminent attack; tail positioned over the back with hairs erect (Ferron 1979) ‡‡ percent time spent in the third of the arena closest to or farthest from the mirror (Front and Back) §§ vocalization of intense threat (Ferron 1979) ¶¶ slow approach towards mirror with back legs stretched behind: characteristic of the exploration of novelty (Ferron 1980)

TABLE 2-2

Final linear mixed model* of offspring growth rate in the nest in North American red squirrels, with female identity as a random effect (N=348 juveniles from 75 females). OF1 is a synthetic variable representing the female's level of activity and exploration.

	DF	F	P
Intercept	1, 264	432.75	< 0.0001
Year	3, 264	31.95	< 0.0001
Parturition date	1, 264	31.09	< 0.0001
Litter size at tagging	1, 264	43.66	< 0.0001
Mass at 1st marking	1, 264	7.21	0.008
OF1	1, 73	2.67	0.11
Year x OF1†	3, 264	14.46	< 0.0001

* Initial model also included as fixed effects grid, sex, mother's age, MIS1, year x MIS1, and OF1 x MIS1, which were removed during model selection with $P > 0.05$.

TABLE 2-3

Final generalized linear mixed model* of juvenile survival in the nest (from shortly after birth until shortly before emergence) for North American red squirrels, with female identity as a random effect (N=517 juveniles from 79 females). MIS1 is a synthetic variable representing the female's aggressiveness.

	DF	t	P
Intercept	431	4.95	<0.0001
2003	431	-0.76	0.45
2004	431	1.87	0.06
2006	431	-0.52	0.60
Parturition date	431	8.17	<0.0001
MIS1	77	-2.98	<0.0001
2003 x MIS1†	431	1.64	0.10
2004 x MIS1	431	2.58	0.01
2006 x MIS1	431	2.19	0.03

* Initial model also included as fixed effects: grid, litter size at birth, mother's age, juvenile sex, mass at first measurement, OF1, year x OF1, and OF1 x MIS1, and these variables were removed during model selection with $P > 0.05$.

TABLE 2-4

Final generalized linear model* of juvenile overwinter survival in North American red squirrels (N=124 juveniles). Female identity, when included as a random effect in a GLMM, explained 0% of the variation and is therefore not included in this model. MIS1 is a synthetic variable representing the female's aggressiveness, and 'bequeathed' indicates that the juvenile was given a territory by its mother.

	LR χ^2	DF	P
Year	0.49	2	0.78
Parturition date	6.31	1	0.01
MIS1	5.53	1	0.02
Bequeathed	4.39	1	0.04
Year x MIS1†	8.39	2	0.02

* Initial model also included as fixed effects: grid, juvenile sex, mother's age, OF1, year x OF1, and OF1 x MIS1, and these variables were removed during stepwise backwards elimination model selection with $P > 0.05$.

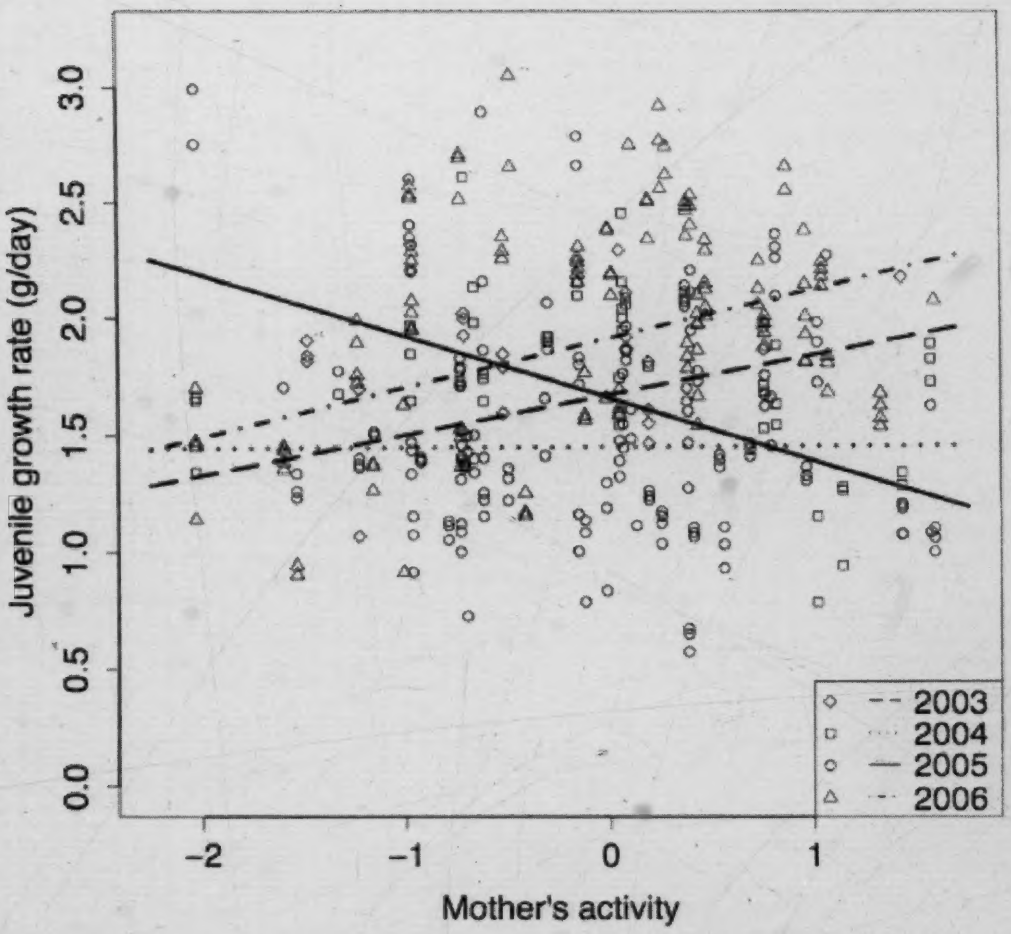

FIGURE 2-1. The nestling growth rate of North American red squirrels depends on the activity level of the mother in an open field behavioural trial and varies by year. See Table 2-2 for details of the linear mixed model.

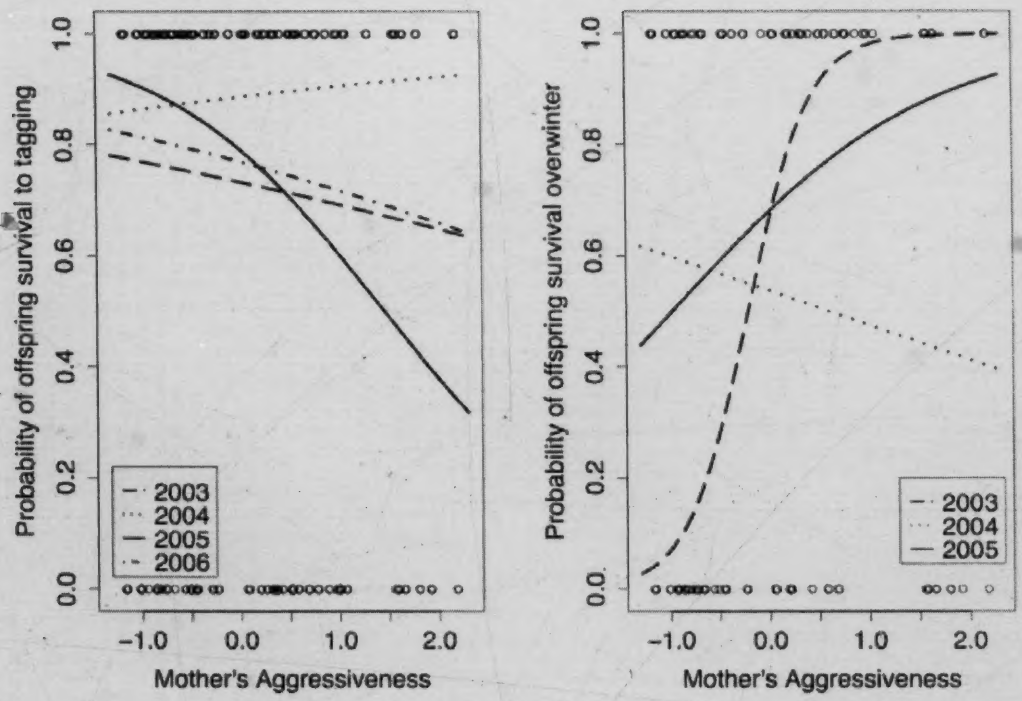

FIGURE 2-2. **(a)** The survival of juvenile North American red squirrels from birth until 25-30 days of age, shortly before emergence, depends on the aggressiveness of their mother and varies by year. **(b)** The overwinter survival of juveniles from weaning until May 1st of the following year also depends on the mother's aggressiveness and varies by year. See Tables 2-3 and 2-4 for details of the models.

CHAPTER III

PERSONALITY, HABITAT USE, AND THEIR CONSEQUENCES FOR SURVIVAL IN NORTH AMERICAN RED SQUIRRELS

INTRODUCTION

Individuals of many species behave in a characteristic manner, such as by being aggressive, shy, or active in a variety of contexts (Wilson *et al.* 1994; Sih *et al.* 2004). This tendency of an individual to behave in a predictable way is referred to as its personality (Gosling 2001), temperament (Réale *et al.* 2007), or behavioural syndrome (Sih *et al.* 2004). Personality may be reflected in many aspects of an animal's behaviour and ecology, including its habitat use, interactions with conspecifics, and willingness to take risks. For example, highly exploratory individuals tend to disperse farther than less exploratory individuals (Fraser *et al.* 2001; Dingemanse *et al.* 2003; Bremner-Harrison *et al.* 2004), and social individuals move away from low density populations or groups and towards high density populations, while asocial individuals do the opposite (Svendsen 1974; Cote & Clobert 2007). Additionally, individuals in populations that are invading new areas (Martin & Fitzgerald 2005), and individuals living in human-disturbed areas (Martin & Réale 2007) tend to be more bold than those in either established populations, or undisturbed habitats.

Personality can affect fitness via both reproductive success and survival (Réale & Festa-Bianchet 2003; Biro *et al.* 2004; Bremner-Harrison *et al.* 2004; Dingemanse *et al.* 2004; Both *et al.* 2005; Sinn *et al.* 2006; Boon *et al.* 2007). The maintenance of variation in personality within a population is not well understood, but may result from

balancing selection due to variable selection pressures (Mangel 1991; Boon *et al.* 2007; Penke *et al.* 2007), or to differences in life-history strategy that affect risk-taking behaviours (Biro *et al.* 2004; Stamps 2007; Wolf *et al.* 2007). For example, the willingness to take risks, such as by intruding on the territories of neighbours or moving long distances, may lead to some of the observed fitness consequences of personality by affecting an individual's habitat use (Fraser *et al.* 2001; Biro *et al.* 2004; Bremner-Harrison *et al.* 2004). The exploration of the habitat surrounding an individual's territory may be both beneficial and hazardous. Extra-territorial movements may be used to evaluate potential mates or seek extra-pair copulations (Neudorf *et al.* 1997; Pedersen *et al.* 2006), to gain knowledge of the quality of nearby habitat and territories (Bruinzeel & van de Pol 2004; Fedy & Stutchbury 2004), or as foraging opportunities when food is scarce (Fedy & Stutchbury 2004). However, moving through unfamiliar areas also increases the risk of predation (Metzgar 1967; Larsen & Boutin 1994; Fraser *et al.* 2001), and being absent from the home territory may result in the loss of cached food to pilfering (Gerhardt 2005) or the loss of offspring to predation (Schmidt & Whelan 2005). Therefore, there may be a trade-off associated with being risk-averse or risk-prone in terms of extra-territorial movements.

An individual's willingness to enter a baited trap may be another indication of its propensity for risk-taking, because it accepts the risks associated with trapping and handling in order to obtain a food reward (Réale *et al.* 2000). Tuyttens *et al.* (1999) found that individual European badgers (*Meles meles*) tended to be either trap-happy (captured 3 times out of 3 trapping sessions) or trap-shy (captured 0 out of 3 times). Réale *et al.* (2000) found both individual consistency and yearly differences in the

number of captures in bighorn ewes (*Ovis canadensis*). Since there are consistent individual differences in the likelihood of entering a trap, and these differences are correlated to other dimensions of personality, such as docility and other measures of boldness (Wilson *et al.* 1993; Réale *et al.* 2000), individual trappability could be considered as a measure of risk-taking.

North American red squirrels (*Tamiasciurus hudsonicus*) are diurnal tree squirrels that defend individual food-based territories year-round with a central cache, or midden, as its physical and activity centre (Gurnell 1984; McAdam *et al.* 2007). At low population densities, squirrels may also defend several secondary middens. Parental care is solely maternal, and mothers sometimes bequeathal territories, by giving part or all of their territory to one or more of their offspring, which increases the offsprings' probability of overwinter survival (Price *et al.* 1986; Boutin & Schweiger 1988; Boutin *et al.* 1993; Price & Boutin 1993; Berteaux & Boutin 2000; Boutin *et al.* 2000; Boon *et al.* 2007). Activity, aggressiveness, struggle rate, and breathing rate during handling are correlated in a proactive-reactive behavioural syndrome in this population (Boon *et al.* 2007).

In this study, we investigated whether risk-taking of female red squirrels, in the forms of trappability and extra-territorial movements, was related to their personality measured via behavioural trials. We used trapping data to obtain three proxies of risk-taking behaviour and related them to the individual's activity and aggressiveness. We predicted that increasing activity and aggressiveness would be associated with an increase in the total number of captures, in the number of capture locations (an indication of how often the individual intrudes on the territories of others), and in the maximum capture

distance from the individual's primary midden. We also predicted that females may use extra-territorial forays to search for a new territory before bequeathing a territory to their offspring. If so, then individuals that explore more extensively (i.e. are trapped in a greater number of different locations and farther from home) may be more likely to bequeath. However, we predict that these behaviours are costly as well, and are associated with an increased risk of predation.

METHODS

This study was conducted in the summer of 2005 using 71 adult female North American red squirrels as part of a long-term study population near Kluane National Park in southwestern Yukon, Canada (61° N, 138° W). Details of the study population and monitoring techniques are described by Boutin *et al.* (2006) and McAdam *et al.*(2007). Three study grids, two control and one experimental food addition, are staked at 30-metre intervals and the locations of middens are recorded at 15-metre intervals. All individuals on the study grids were marked with numbered ear tags and a unique combination of coloured wires. Their survival and reproduction were monitored through live trapping with Tomahawk traps baited with peanut butter, and behavioural observations. Generally traps were set on every grid six mornings per week between the middle of February and the end of September (2005). The time of day and number of hours per day that traps were open depended primarily on season, as we tried to match trapping to the squirrels' activity patterns; in winter, traps were open during most of the day, while in summer trapping was restricted to the morning (0700h until 1200h or 1300h) and sometimes the

evening (approximately 1900h – 2200h). Traps were checked every 90 minutes and were closed after the target squirrel had been captured. Squirrels were captured as targets on their own territories, and as intruders on the territories of others. Non-breeding, lactating, and post-weaning females were targeted for trapping approximately every two weeks, while pregnant females were targeted every 10 days early in the pregnancy and up to every three days near the end to accurately pinpoint the parturition date.

Field technicians set a variable number of traps on a variable number of middens owned by the target squirrel. One or two traps were set on the primary midden for most individuals, but technicians would set more traps and more middens for individuals that they knew to be hard to capture, or for individuals that they had already targeted without success for one or more days. We have not corrected for this variation in trapping effort because it should act to decrease the variation in trapping success among individuals; those who were hard to trap were targeted more frequently and with greater effort, while those who were frequently caught as intruders were rarely targeted directly. Some squirrels lived on the study grids for longer periods of time than others (due to immigration, emigration or death), and to account for this we included in all trapping analyses an independent variable consisting of the number of days that the individual was present in the study population, calculated as the number of days between the first capture of 2005 and the last sighting, capture, or confirmation of death.

We used three indices of boldness and exploration related to trapping success: the total number of captures, the number of different locations where the individual was captured (regardless of whether those locations were on their territory or not), and the farthest distance from home that the squirrel was captured, measured as the straight-line

distance to its primary midden. Since each squirrel owns between one and three middens, an increasing number of trapping locations indicates that they are intruding on the territories of an increasing number of other individuals. All statistics were performed using R 2.5.1 (R Development Core Team 2006). For all analyses, we used stepwise backwards elimination model selection at $P = 0.05$ with dependent variables standardized to a mean of zero.

Measuring personality

We used two behavioural tests to measure personality, an open field test to quantify behaviours related to activity and exploration (Walsh & Cummins 1976), and a mirror-image stimulation to measure aggressiveness (Svendsen & Armitage 1973). The complete ethogram, descriptions of behaviours, and field and statistical methods are described in detail elsewhere (Boon *et al.* 2007). Briefly, we captured the test subjects on their territory, and placed them in a 60 cm X 80 cm X 50 cm plastic arena with a clear lid, and videotaped their movements and behaviours during the 7.5-minute open field trial, after which we uncovered a mirror on one wall and continued with a 5-minute mirror image stimulation, then released the squirrel. Fifty-five of the 71 squirrels were measured twice at least six weeks apart, and of the remaining 16 individuals, seven died of natural causes, two disappeared and probably also died, and seven were alive but could not be recaptured. The behavioural trials were analysed using The Observer Video-Pro 5.0 software (Noldus Information Technology, 2004, Wageningen, The Netherlands). We measured the percentage of time spent in, frequency of, or latency to perform various behaviours. See Boon *et al.* (2007) for more information.

Using principal components analyses (PCA), separately for the open field and mirror image stimulation, we reduced the measured behavioural variables to a smaller number of synthetic variables. We chose to include only the first principal component from each test in further analyses, as described in Boon *et al.*(2007). In the open field, the first principal component, hereafter activity, explained a total of 33% of the variance, and represents the individual's level of activity and exploration. In the mirror image stimulation, the first principal component, hereafter aggressiveness, explained 45.4% of the total variance. We performed a linear mixed model on the principal component scores to test for effects of date, grid, age, reproductive status, time of day and trial number, with the individual's identity included as a random effect. In the open field, trial number was the only significant fixed effect, with squirrels generally being less active in the second trial than the first ($F = 10.85$, $df = 1, 54$, $P = 0.002$), and this model including identity was significantly better than a restricted linear model without it (Likelihood ratio $= 11.11$, $df = 1$, $P < 0.001$). The repeatability, the proportion of total variance that was due to the individual (Lessells & Boag 1987), of this component was 44.3%. In the mirror image stimulation, there were no significant fixed effects in the final mixed model, which was significantly better than the restricted linear model (Likelihood ratio = 7.84, df $= 1$, $P = 0.005$). The repeatability of this component was 39.0%. We extracted the best linear unbiased predictors (BLUPs) from the final mixed models, which provide predictions of the random effects independent of the other terms in the model, standardized to a mean of zero (Kruuk 2004), and used these values as the individual personality values of activity and aggressiveness in further analyses.

The relationship between personality and trapping success

We tested for correlations among the three indices of trapping success using Kendall nonparametric correlations to determine how these variables are related to each other. We calculated false discovery rates (Benjamini *et al.* 2001) to control for multiple comparisons. To analyse the influence of personality on the total number of captures and the number of different capture locations, we used Generalized Linear Models (GLM) with a negative binomial distribution and a square-root link. We included as independent variables in both models the grid, the squirrel's age, the total number of days that the squirrel was present in the study population, its activity and aggressiveness, and the interaction between activity and aggressiveness. We calculated the proportion of variance explained by the model as r^2 = (null deviance – residual deviance)/null deviance, and partial r^2 for each variable as the change in r^2 when the variable in question was removed from the model.

To model the relationship between personality and the maximum capture distance from a squirrel's primary midden, we used a linear model on square-root transformed distances and included the same independent variables as in the previous two models. We calculated the partial r^2 (adjusted) as above.

We tested whether indices of personality or trappability affected the tendency of females to bequeath territories to their offspring. For the 45 females that had at least one offspring survive to weaning in 2005, we considered them to have bequeathed a territory if at least one of their offspring settled on the natal territory (i.e. settled on a midden that the mother defended previously by giving territorial rattle calls, Smith 1968). We used a binomial GLM with logit link, and age, grid, maximum capture distance, number of

captures per time (i.e. number of captures divided by the number of days present in the population), number of capture locations per time, and activity, aggressiveness, and their interaction as independent variables.

Finally, we investigated whether there were survival costs associated with either personality or capture success. Using binomial GLMs with logit links, we analysed whether females survived until May 1, 2006 (the spring following the study year), and if they died, whether it was due to predation. If the cause of death was not known, it was assumed not to be predation. The independent variables in both initial models were identical to those used in the bequeathal model above.

RESULTS

Individual female red squirrels were captured an average of 21.6 times (range 6 to 48), or 0.13 captures per day present in the population (range 58 to 218 days, and 0.06 to 0.31 captures per day). They were caught at an average of 6.6 different locations (range 1 to 17), and the average maximum captures distance was 136 meters from the primary midden (range 0 to 378 meters).

The total number of captures, the number of capture locations and the maximum capture distance were all significantly correlated to each other (Kendall, $N = 71$, number of captures to number of locations, $\tau = 0.49$, $P < 0.0001$; number of captures to maximum distance, $\tau = 0.17$, $P = 0.03$; number of locations to maximum distance, $\tau = 0.43$, $P < 0.0001$). None of these correlations was affected by the calculation of false discovery rates (Benjamini *et al.* 2001).

After correcting for the number of days that an individual spent in the population, squirrels that were more active and lived on the food supplemented grid were captured a greater number of times (Table 3-1, Fig. 3-1a), but age, aggressiveness and the interaction between activity and aggressiveness were not significant ($P > 0.5$). The r^2 for the selected model was 0.29. Squirrels that were more active and squirrels that were older were also captured at a greater number of different locations (Table 3-1, Fig. 3-1b), after correcting for the number of days, but grid, aggressiveness, and the interaction between activity and aggressiveness were removed from the model with $P > 0.2$. The r^2 for the selected model was 0.19. The maximum capture distance was significantly related to an interaction between activity and aggressiveness (Table 3-1). Activity and aggressiveness are correlated ($r = 0.54$) in this population (Boon *et al.* 2007), and maximum capture distance increases with both of these traits, such that increasing both leads to a larger increase in maximum capture distance than does increasing either one independently. Individuals from one of the two control grids also tended to be caught farther from their primary midden than other squirrels, but age and time spent in the population were not significant ($P > 0.1$). The adjusted multiple r^2 for the selected model was 0.16.

Forty-five squirrels had at least one offspring survive to weaning, and 31 of them bequeathed a territory while 14 did not. Squirrels that were trapped at a greater number of different middens per time present in the population were more likely to bequeath a territory to their offspring (LR $\chi^2 = 7.00$, df = 1, $P = 0.008$; Fig. 3-2), after controlling for grid (LR $\chi^2 = 25.00$, df = 2, $P < 0.001$) and age (older squirrels were less likely to bequeath; LR $\chi^2 = 6.36$, df = 1, $P = 0.01$). There was no effect of the number of captures

per time, the maximum capture distance, activity, aggressiveness, or the activity by aggressiveness interaction (all removed with $P > 0.1$).

Forty-five squirrels survived until the following spring and 26 died, of which six were confirmed predations. Squirrels that were older and squirrels that were more active were more likely to die (age: LR $\chi^2 = 8.77$, df = 1, $P = 0.003$; activity: LR $\chi^2 = 5.52$, df = 1, $P = 0.02$; Fig. 3-3a), and of those that died, the ones that had a greater maximum capture distance were more likely to die of predation (LR $\chi^2 = 5.79$, df = 1, $P = 0.016$; Fig. 3-3b). The grid, number of captures per time, number of capture locations per time, aggressiveness, and the interaction of activity by aggressiveness were not significant in either model. Maximum capture distance was also not significant for the survival model, and age and activity were not significant for the predation model (all $P > 0.09$).

DISCUSSION

This study suggests that personality can influence risk-taking and habitat use, and provides further evidence for fitness consequences of personality in wild populations. In female red squirrels, increasing activity was associated with an increasing propensity to enter traps, to intrude on the territories of others, and to move farther from their own territory, all of which seem to represent risk-taking behaviours. The maximum capture distance also increased with increasing aggression, but we detected no relationship between aggressiveness and the number of captures or number of capture locations. Females who were trapped on a greater number of other middens were more likely to bequeath a territory to their offspring, but more active squirrels were less likely to survive

until the spring of the following year, and females who were captured farther from their primary midden were more likely to be predated.

For an adult female red squirrel, there are both costs and benefits associated with using the habitat surrounding her territory. There are survival costs associated with high activity, and travelling far from the primary midden results in a higher chance of being depredated. Juvenile red squirrels are also more likely to be killed while off their natal territory (Larsen & Boutin 1994; Stuart-Smith & Boutin 1995), and transient white-footed mice (*Peromyscus leucopus*) are more likely to be depredated than are residents (Metzgar 1967). In reintroduced swift fox (*Vulpes velox*), bold individuals both move greater distances from the point of release, and are less likely to survive (Bremner-Harrison *et al.* 2004). The chances of being killed when off-territory may be higher than when on-territory owing to lower familiarity with escape routes and refuges, being engaged in exploratory behaviours that reduce vigilance, and being vigilant for territory owners as well as for predators (Metzgar 1967). Intruding on the territories of others may also increase predation risk due to increased conspicuousness and decreased vigilance during chases (Price *et al.* 1990). Resident squirrels generally respond more strongly to the calls of strangers than to the calls of neighbours (Price *et al.* 1990), so the risk of a chase may also increase with distance from home as the squirrel begins to encounter unfamiliar conspecifics. Alternatively, individuals that spend more time off-territory may be inherently less cautious and engage in riskier behaviour whether they are on- or off-territory; for example, juvenile red squirrels that spend less time resting or vigilant and more time in exposed locations are more likely to be depredated (Stuart-Smith & Boutin 1995; Anderson & Boutin 2002). Survival may also be affected by energetic factors not

considered here: active squirrels (that are generally also aggressive) may have higher resource requirements due to higher metabolic rates, leading them to be more prone to starvation (Ros *et al.* 2004; Ros *et al.* 2006; Tobler *et al.* 2007). There could also be other risks associated with leaving the territory unattended for long periods of time, such as by travelling very long distances or by being in a trap, including the predation of offspring (Schmidt & Whelan 2005) or pilfering from food caches (Gerhardt 2005). However, we did not measure these in this study.

The benefits to exploring off-territory may include knowledge of other individuals and the availability of territories and resources. Squirrels sometimes change territories; in females, this occurs most frequently after bequeathing her former territory to an offspring, although she may also bequeath just a portion and stay on the remainder herself (Price *et al.* 1986; Boutin & Schweiger 1988; Boutin *et al.* 1993; Price & Boutin 1993; Berteaux & Boutin 2000; Boutin *et al.* 2000). In the current study, females who were caught in a greater number of different locations were more likely to bequeath a territory to their offspring, and therefore may have been prospecting for a new territory. Juveniles that receive a territory from their mother are more likely to survive the winter (Boutin *et al.* 1993; Berteaux & Boutin 2000; Boon *et al.* 2007), and so bequeathal has a positive effect on the mother's fitness. In other species, an individual's extra-territorial exploration has also been observed to provide important knowledge regarding the quality of nearby habitat and territories, as well as foraging opportunities (Bruinzeel & van de Pol 2004; Fedy & Stutchbury 2004). In collared flycatchers (*Ficedula albicollis*), individuals use public information regarding the breeding success of conspecifics to assess the quality of breeding habitat and inform future breeding-site decisions (Doligez

et al. 2002), and movements off-territory may allow the gathering of such information. Gerhardt (2005) observed very high rates of food pilfering from the caches of other individuals in an eastern population of red squirrels, and so extraterritorial movements may also permit the stealing of food. In birds, extra-territorial movements can also facilitate extra-pair copulations or permit the evaluation of potential mates (Neudorf *et al.* 1997; Pedersen *et al.* 2006). During the breeding season, male red squirrels move large distances in search of estrous females, and both sexes may seek information on the quality of potential mates (J.E. Lane, unpublished data).

There are several potential biases in our data, but we believe that they would act to reduce rather than increase the probability of finding significant effects of personality on risk-taking behaviours, or of either of these on life history parameters. We did not correct for variation in trapping effort, as discussed previously, but as a result, the true variations in number of captures between trap-shy and trap-happy individuals should be larger than seen here. Another potential bias stems from spatial aspects of our grids. Individuals in the centre of a grid would presumably have more opportunities to encounter traps than would individuals on the periphery, who would encounter traps when moving towards the centre of the grids but not when moving away. However, for the most part our grids are surrounded by unsuitable habitat (e.g. wetlands and meadows) and so we expect that there is relatively little movement in those directions (McAdam *et al.* 2007). Additionally, as there is no indication that proximity to the edge of a grid is related to personality (A. Boon, unpublished data), this should also reduce the probability of detecting effects in our models. Similarly, the true maximum distances travelled from home are likely greater than those detected, given the stochastic nature of this

measurement and the low probability of a squirrel encountering a trap when at its greatest displacement. Another potential bias relates to our use of trapping data to measure exploration off-territory rather than telemetry or another method that allows the random sampling of behaviour. Our three measures of risk-taking are all, in a sense, estimations of the willingness of the squirrel to enter a trap, and as such are not independent measures. There could be individuals that are generally trap-shy but also move long distances from their territories that we don't detect. If this were the case, then the increased risk of predation that we detected may be related to aspects of the squirrel's behaviour other than distance moved, as discussed previously. However, our results are consistent with those of other studies indicating that predation risk increases when off-territory (Metzgar 1967; Larsen & Boutin 1994; Stuart-Smith & Boutin 1995).

A squirrel's personality affects her habitat usage as well as her fitness. Increasing activity tends to be associated with an increasing tendency to be risk-prone, and although those individuals had a lower chance of survival in the time period of this study, they may have gained other advantages such as knowledge about habitat quality and vacant territories. This potential trade-off in risk-taking behaviours suggests that one strategy is not always better than another, and so multiple selection pressures may act to maintain variation in personality via balancing selection (Boon *et al.* 2007; Penke *et al.* 2007) and/or correlations with life history strategies (Stamps 2007; Wolf *et al.* 2007).

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TABLE 3-1

Three aspects of trappability are significantly affected by personality in adult female North American red squirrels in Yukon, Canada. All initial models included activity, aggressiveness, and their interaction, as well as grid, age, and the number of days that the squirrel was present in the study population, and non-significant terms were removed using stepwise backwards model selection with $P > 0.05$. Number of captures and number of capture locations were analysed using a GLM with negative binomial distribution. The r^2 for the selected models was 0.29 and 0.19 respectively. Maximum distance from home was a linear regression with a square-root transformed response variable, and the adjusted r^2 for the selected model was 0.16.

Number of captures	**Partial r^2**	**LR χ^2**	**DF**	**P**
Activity[1]	0.09	8.93	1	0.003
Grid	0.15	14.68	2	0.0006
Days present	0.21	21.27	1	<0.0001
Number of capture locations	**Partial r^2**	**LR χ^2**	**DF**	**P**
Activity [2]	0.07	6.25	1	0.01
Age	0.05	4.14	1	0.04
Days present	0.10	8.17	1	0.004
Maximum capture distance	**Partial r^2**	**F**	**DF**	**P**
Activity	0.03	2.37	1	0.13
Aggressiveness	0.01	0.50	1	0.48
Activity*Aggressiveness[3]	0.07	6.09	1	0.02
Grid	0.10	5.13	2	0.009

1. coefficient = 0.28 ± 0.09
2. coefficient = 0.20 ± 0.08
3. coefficient = 1.50 ± 0.61

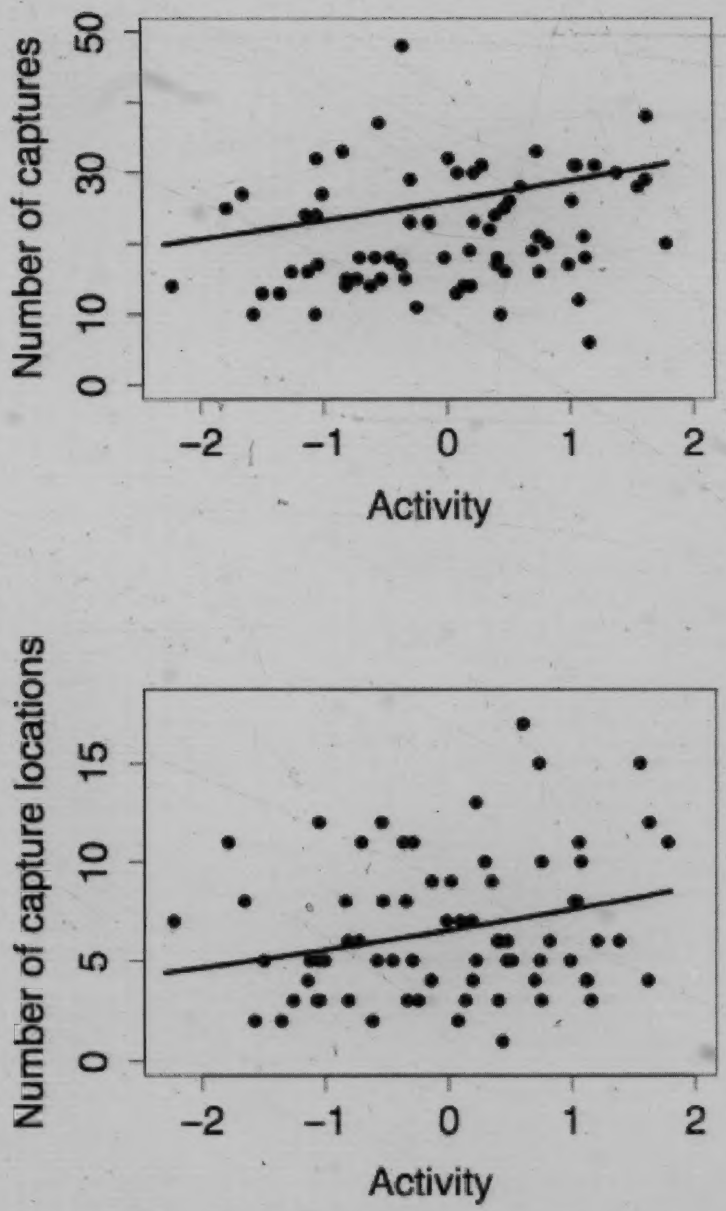


FIGURE 3-1. In female North American red squirrels, increasing activity in an open field behavioural trial is associated with **(a)** an increasing number of trapping events and **(b)** an increasing number of different capture locations, between February and September, 2005, after correction for the number of days present in the population.

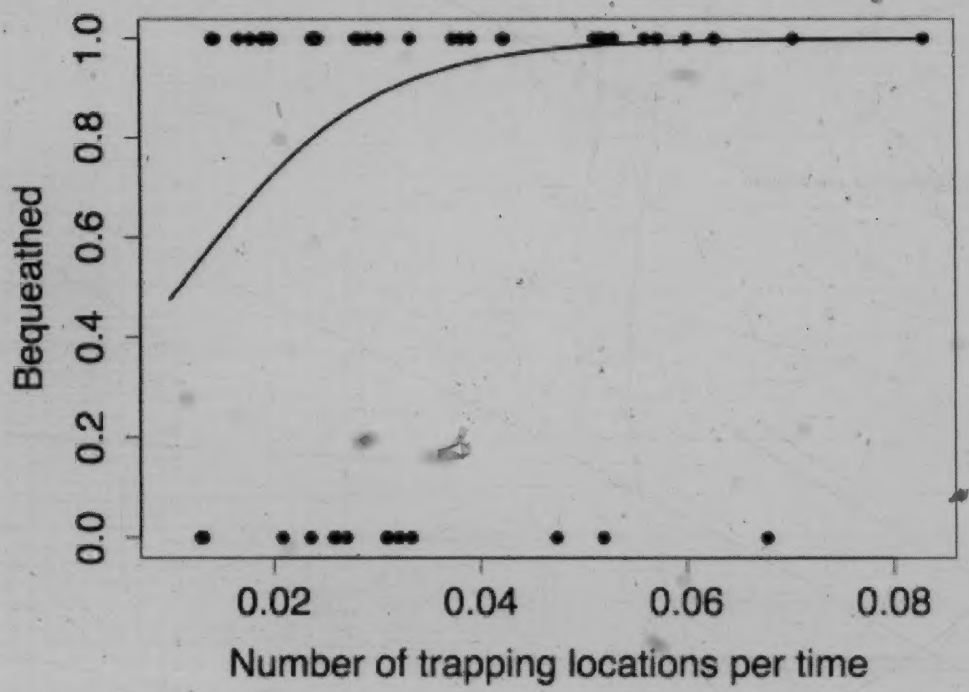
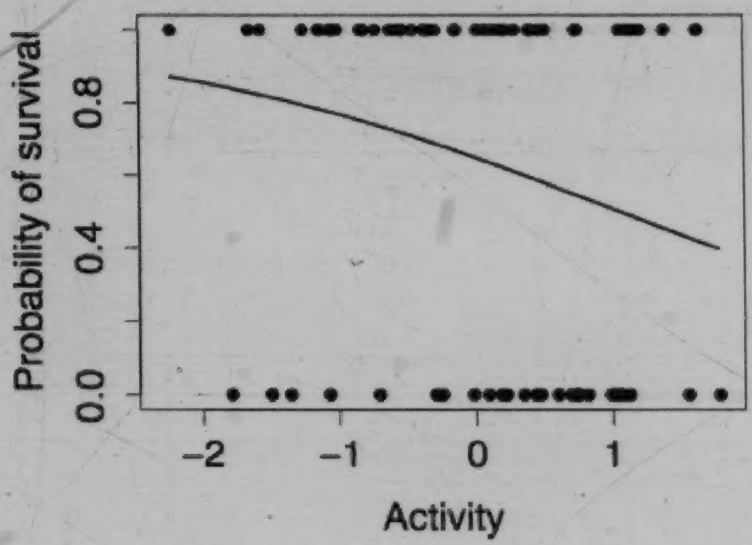


FIGURE 3-2. Female North American red squirrels that were trapped at a greater number of different locations were more likely to bequeath a territory to their offspring.



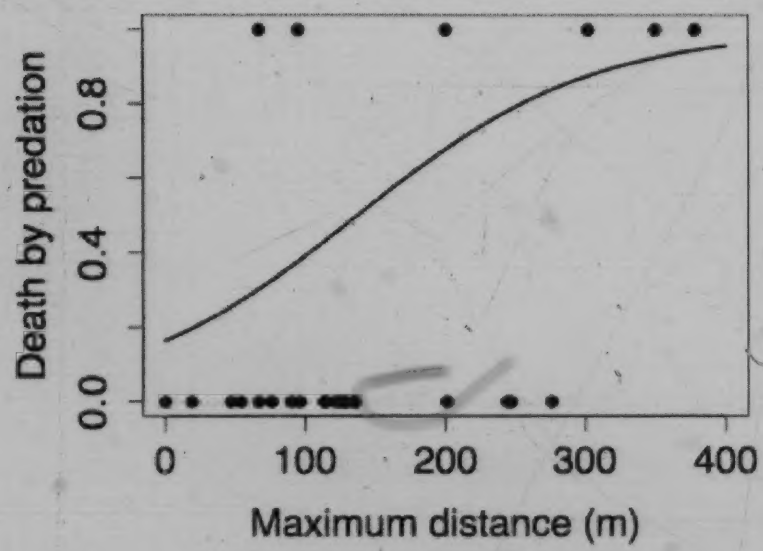


FIGURE 3-3. **(a)** More active female North American red squirrels were less likely to survive until the following spring (from June 2005 to May 2006). **(b)** Females who were captured farther from their home territory in the summer of 2005 were more likely to be predated than to die of other causes.

CHAPTER IV

GENERAL DISCUSSION AND CONCLUSIONS

Animals in wild populations have consistent individual personalities that affect their behaviour, life history and fitness in many different ways. However, few empirical studies so far have investigated more than one or two traits at a time, and rarely in more than one year. The small scale of these studies has led to only limited understanding of the effects of personality on life history and the implications for fitness and selection.

The primary objective of this study was to investigate the fitness consequences of personality using multiple life history traits to evaluate whether selection could actively maintain variation in personality within a population (Penke *et al.* 2007). I approached this question by combining field studies of personality with long-term life history data in North American red squirrels. Although personality can affect many different aspects of an animal's ecology, I chose to focus on two aspects in particular. First, I investigated the influence of maternal personality on offspring fitness in multiple years with varying levels of resource abundance, and second, I compared individual personality to risk-proneness and correlated life history trade-offs. This study provides a broad view of the fitness consequences of personality in a wild population and demonstrates its relevance to ecology and evolution.

SUMMARY OF RESULTS

Female North American red squirrels have distinctive individual personalities that can be described according to their tendency to be active in an open-field behavioural trial and aggressive in a mirror-image stimulation test. These traits are also correlated to struggle rate and breathing rate during handling, and to risk-taking behaviours such as trappability and the tendency to intrude on the territories of other individuals. This combination of traits is typical of the proactive-reactive behavioural syndrome (Koolhaas *et al.* 1999; Sih *et al.* 2004).

The personality of a female squirrel influences both the growth rate and the survival of her offspring in the nest, as well as the survival of her offspring overwinter. However, the direction and the magnitude of the selection pressures on personality via life-history vary among years. Food abundance may be important in influencing the relationship between offspring growth and maternal activity; more active mothers tended to have faster-growing offspring in years following large cone crops, and slower-growing offspring following small cone crops. However, more research is needed to determine if this pattern repeats itself over a greater number of years, and if food abundance is actually the cause. The survival of offspring was affected by the aggressiveness of the mother, and the direction and magnitude of the relationship changed between years as well, but in this case there did not seem to be a relationship with food abundance. Population density, maternal behaviour, metabolic differences, and the heritability of personality may play roles in this correlation, but further study is needed. In addition to yearly changes in selection pressures, it seems that there may be antagonistic effects of

personality traits at different life history stages. For example, maternal aggressiveness tended to have opposite effects on juvenile survival in the nest and overwinter.

A female's tendency to take risks, such as by entering traps, intruding on the territories of others, and moving long distances off-territory, were correlated with personality as measured in behavioural trials, and were associated with a fitness tradeoff. Females that were trapped at a greater number of different middens were more likely to bequeath a territory to their offspring, increasing the offsprings' chances of overwinter survival. However, more active females were less likely to survive until the following spring, and females that were trapped at greater maximal distances from their home territory were more likely to be killed by a predator than to die from other causes. It seems then that personality results in a fitness trade-off, such that females showing high activity have increased reproductive fitness but reduced survival, while females with low activity have the opposite. If the resolution of this trade-off is associated with different life history strategies, then it may act to maintain variation in personality through its association with risk-taking behaviours (Stamps 2007; Wolf *et al.* 2007). A trade-off between early primiparity and a long lifespan has previously been identified in this population (Descamps *et al.* 2006), which could be associated with differences in personality and risk-proneness, but further research is needed to determine if this is the case.

In the course of my thesis research, I found support for both of the current theoretical models for the maintenance of variation in personality. Selection pressures vary in direction and magnitude among years, possibly in association with environmental heterogeneity, and personality has different effects at different life history stages. Both of

these factors indicate that balancing selection could be actively maintaining variation in personality. Additionally, personality is associated with risk-taking behaviours that lead to a fitness trade-off, although it is not yet known if these behaviours are also associated with different life history strategies. Because I cannot show that individuals with differing personalities have equivalent fitness overall, it cannot be determined with certainty at this time if balancing selection due to environmental heterogeneity or antagonistic pleiotropy could act to maintain variation in the long run (Penke *et al.* 2007). However, selection pressures on personality change between years such that different phenotypes appear to be favoured in different conditions, indicating that in any case, there is not a single personality type that is most successful at all times.

FUTURE DIRECTIONS

The field of animal personality is still quite new, and there are many questions that remain to be answered. The particular strengths of the Kluane red squirrel population for this research are the availability of pedigree information and of multiple years of life history data for individuals. As such, there is still much to be gained by studying red squirrel personality, including questions that have arisen based on the results of my thesis research, and new avenues of research that would benefit from the insights that could be provided by this well-studied population.

My results suggest that both balancing selection and correlations with life history trade-offs may act to maintain variation in personality in this population. However, I could not demonstrate that the yearly patterns in growth rate were related to food supply,

and I could not follow individuals throughout their lifetime in order to determine whether all individuals, regardless of their personality, had equal fitness overall. Both of these questions would require many years of study, but I believe that they would be worth pursuing. The food supplementation experiment currently underway may be able to provide unique insight into the role of resource abundance in influencing the success of individuals with different personalities.

Additionally, the mechanisms of the associations between personality and life history traits remain speculative in some cases, and further research may help to clarify the causes of some of the observed patterns. In particular, I think that the following avenues of research are important.

- Is personality heritable in this population? Is maternal or offspring personality more important in determining offspring survival overwinter?
- Is metabolic rate related to personality? Do aggressive individuals have higher minimum resource requirements? Does this affect their reproductive success differently in years of low versus high food abundance? Do the metabolic rates of offspring show the same pattern?
- How does personality influence maternal behaviour? Do some females provide more or better care to their offspring? Does this interact with the personalities or metabolic rates of the young to affect a mother's reproductive success?

I also showed that personality is related to a female's tendency to take risks in red squirrels, and that risk-taking leads to a fitness trade-off. The next step would be to determine whether risk-taking is related to life history strategies in such a way that it maintains variation in personality. It would also be interesting to determine whether the

choice of life history strategy is influenced by differences in resource requirements, as discussed previously.

There are also a few other areas of research that I think are interesting and particularly well suited to study in red squirrels because their ecology is well-studied.

- Does male personality vary in similar ways to female personality? Do males tend to be more or less active or aggressive on average? Does personality affect their attendance at mating chases or their ability to gain copulations? Do particular maternal-paternal personality pairings create better offspring than others?
- Does personality influence an individual's access to resources? Do aggressive individuals have larger or better territories?
- Do more active juvenile red squirrels tend to disperse farther than less active juveniles? Do they make more frequent or longer exploratory forays?
- How do maternal effects influence the development of personality? Do the offspring of active or aggressive mothers have greater exposure to androgens prenatally, and how does this influence their personality later in life?

Research on animal personality is an exciting and fast-moving field. This is one of the first studies to make use of a long-term study population to investigate the influence of personality on individual fitness. Although we still know relatively little regarding the maintenance of variation in personality, I hope that this study has indicated useful avenues for future research in order to increase our understanding of this topic, as well as demonstrated that considerations of animal personality can be important to many different areas of ecology.

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APPENDIX 1

MEAN VALUES AND RANGES FOR BEHAVIOURAL TESTS

OPEN FIELD TEST

Behaviour	Units	Mean	Minimum	Maximum
Pellets	Number	11.7	0.0	43
Jump	Rate (number / min)	3.8	0.1	17.7
Hole	Rate (number / min)	1.7	0.0	6.7
Walk	% time	16.2	0.6	47.7
Sniff	% time	7.2	0.0	25.0
Scan	% time	11.8	0.3	41.7
Still	% time	29.4	0.1	99.1
Rear	% time	8.4	0.0	33.2
Chew	% time	4.4	0.0	49.3
Hang	% time	16.2	0.0	75.4
Groom	% time	3.5	0.0	32.1

MIRROR IMAGE STIMULATION

Behaviour	Units	Mean	Minimum	Maximum
Attack	Rate (number / min)	0.56	0.0	5.2
Crouch	Rate (number / min)	0.68	0.0	6.4
Front	% time	19.2	0.0	99.7
Back	% time	40.3	0.0	100.0
Attack latency	Latency (s)	214.9	0.3	300.0
Approach latency	Latency (s)	140.6	0.0	300.0
Grunt	% time	1.2	0.0	40.4
Stretch	% time	1.0	0.0	9.7

HANDLING TEST

Behaviour	Units	Mean	Minimum	Maximum
Struggle rate	Seconds/ 30 seconds	11.6	0.0	30.0
Breathing rate	Breaths/ 10 seconds	30.0	15.0	48.0